Stability Analysis of Wangersky-Cunningham Model with Constant Effort of Harvesting

Syamsuddin Toaha[*]

Abstrak

In this paper we consider another predator-prey model with time delay which is called the Wangersky-Cunningham model. In this model, the rate of change of the predator population depends on the numbers of prey and predator present at some previous time. The model is then improved by considering a constant effort of harvesting into the growth rate of the prey and predator populations. The method use in this analysis is linearization the model around the equilibrium point and then inspecting the eigenvalues to determine the stability. We found that there exists a positive equilibrium point for the model with and without harvesting. The time delay can induce instability and Hopf bifurcation can also occur. Some plots of trajectories of the prey and predator populations are also given.

Kata Kunci: Wangersky-Cunningham model, time delay, constant effort harvesting, Hopf bifurcation.

1. Introduction

The dynamics relationship between predators and their prey has long been and will continue to be one of the dominant themes in both ecology and mathematical ecology due to its universal existence and importance, Berryman (1992). This problem may appear simple mathematically at first sight, in fact, often very challenging and complicated.

A rather characteristic behavior of the predator-prey dynamics is the often observed oscillatory phenomenon of the population sizes. Some predator-prey models which are considered in Beretta and Kuang (1998) provide the same kind of mechanisms of producing oscillatory solutions. Another common mechanism of oscillatory solution is to introduce time delays in the models, which is a more realistic approach to the understanding of the predator-prey dynamics.

A simple and natural way to do oscillation is to incorporate a single discrete delay into predator equations, Beretta and Kuang (1998). Lotka-Volterra type predator-prey model with Michaelis-Menten type functional response and hybrid type of predator-prey model as well known as Holling-Tanner predator-prey model have been developed by incorporating the time delay in the predator equation.

Liu and Wang (2004) have considered a non autonomous predator-prey diffusion system with Holling III functional response and a continuous time delay and the result showed that the system is persistent under any diffusion rate effect and the positive periodic solution is globally asymptotically stable.

Li and Kuang (2001) have studied the sufficient conditions for the existence of the positive periodic solutions in periodic delayed Gause-type predator-prey systems and the results indicate that when both seasonality and time delay are present, the seasonality is often generating

---

[*] *Jurusan Matematika, Fakultas Matematika dan Ilmu Pengetahuan Alam,*
  Universitas Hasanuddin, email: syamsuddint@yahoo.com

Syamsuddin Toaha

force for the often observed fluctuation in population densities, including the inherently oscillatory predator-prey dynamics.

A model with time delay in a predator-prey system has been considered in Qiu and Mitsui (2002) and the results show that the system is permanent under some appropriate conditions and sufficient conditions are established for the global asymptotic stability of the positive equilibrium point of the system.

Gourley and Kuang (2004) have formulated a general and robust predator-prey model with stage structure with constant maturation time delay and performed a systematic mathematical and computational study. The results indicated that if the juvenile death rate is nonzero, then for small and large values of maturation time delay, the population dynamics takes the simple form of a globally attractive steady state.

In a predator-prey model, Kar (2003) has considered and discussed the selective harvesting of fishes by incorporating a time delay in the harvesting term and the results showed that the time delay can cause a stable equilibrium point to become unstable and even a switching of stabilities.

In this paper, we consider another predator-prey model with time delay which is called the Wangersky-Cunningham model. In this model, the rate of change of the predator population depends on the numbers of prey and predator present at some previous time. We next consider the constant effort of harvesting into the model. In the analysis, the sufficient condition for the existence of the positive equilibrium point and harvesting level are considered and also the time delay margin is studied.

2. Wangersky-Cunningham Model

In the study of predator – prey model, Volterra in Kuang (1993) has investigated the model

$$\frac{dx(t)}{dt} = x(t)\left(a - bx(t) - \int_{-\tau}^{0} F_1(\theta) y(t+\theta)d\theta \right)$$
$$\frac{dy(t)}{dt} = y(t)\left(-\delta + cx(t) + \int_{-\tau}^{0} F_2(\theta) x(t+\theta)d\theta \right),$$

where x and y are the size of prey and predator, respectively, and all parameters and functions are nonnegative. For similar interactions, Wangersky and Cunningham in Kuang (1993) also use the model

$$\frac{dx(t)}{dt} = rx(t)\left(1 - \frac{x(t)}{K} \right) - \alpha x(t) y(t)$$
$$\frac{dy(t)}{dt} = -cy(t) + \beta x(t-\tau) y(t-\tau)$$

(1)

for predator–prey model with time delay. The parameter r is the rate of increase of the prey population, c is the death rate of the predator population, α is the coefficient of effect of predation on x, β is the coefficient of effect predation on y, τ is a positive time delay, and K represents the carrying capacity of the prey population when there is no interaction between prey and predator. The time delay $\tau \geq 0$ is a constant based on the assumption that the change rate of the predator population depends on the numbers of prey and of predator present at a certain previous time. When we put $\tau = 0$ in model (1), the model is reduced to a predator–prey model

Syamsuddin Toaha

$$\frac{dx(t)}{dt} = rx(t)\left(1 - \frac{x(t)}{K}\right) - \alpha x(t)y(t)$$

$$\frac{dy(t)}{dt} = -cy(t) + \beta x(t)y(t)$$

which has been analyzed in the previous chapter, see also Toaha *et al.* (2007). This model has an equilibrium point $\left(x^*, y^*\right) = \left(\frac{c}{\beta}, \frac{r(K\beta - c)}{\alpha\beta K}\right)$ which is globally asymptotically stable when $K\beta - c > 0$.

Martin and Ruan (2001) have analyzed the Wangersky-Cunningham model where the prey is harvested with constant quota. The considered model is

$$\frac{dx(t)}{dt} = rx(t)\left(1 - \frac{x(t)}{K}\right) - \alpha x(t)y(t) - H$$

$$\frac{dy(t)}{dt} = -cy(t) + \beta x(t-\tau)y(t-\tau),$$

where H is a positive constant, or well known as constant quota of harvesting. The positive equilibrium point of the model is $\left(x_e, y_e\right)$ given by $x_e = \frac{c}{\beta}$ and $y_e = \frac{rc\beta K - rc^2 - H\beta^2 K}{\alpha c \beta K}$.

They showed that the time delay can induce instability and oscillations via Hopf bifurcations and switching of stability occurs. Their analysis is also valid when $H = 0$.

3. Wangersky-Cunningham Model with Constant Effort of Harvesting

We consider the predator and prey populations in model (1) where the two populations are subjected to constant effort of harvesting. The model with harvesting is as follows

$$\frac{dx(t)}{dt} = rx(t)\left(1 - \frac{x(t)}{K}\right) - \alpha x(t)y(t) - E_x x(t)$$

$$\frac{dy(t)}{dt} = -cy(t) + \beta x(t-\tau)y(t-\tau) - E_y y(t). \tag{2}$$

For analysis we assume that $E = E_x = E_y$. Here, we assume that the two populations are harvested by applying the same effort. For example in fishing, the fisheries use the same net and boat. The positive constant E is the effort of harvesting. Then the model becomes

$$\frac{dx(t)}{dt} = rx(t)\left(1 - \frac{x(t)}{K}\right) - \alpha x(t)y(t) - Ex(t)$$

$$\frac{dy(t)}{dt} = -cy(t) + \beta x(t-\tau)y(t-\tau) - Ey(t). \tag{3}$$

The model can be rewritten as

$$\frac{dx(t)}{dt} = r_1 x(t)\left(1 - \frac{x(t)}{K_1}\right) - \alpha x(t) y(t)$$

$$\frac{dy(t)}{dt} = -c_1 y(t) + \beta x(t-\tau) y(t-\tau)$$

(4)

where $r_1 = r - E$, $K_1 = \dfrac{(r-E)K}{r}$, and $c_1 = c + E$. We assume that $r > E$. This assumption is made to guarantee the intrinsic growth of prey population is greater than the effort of harvesting so that the population can increase in size. The equilibrium points of model (4) are $E_0 = (0, 0)$,

$E_1 = (K_1, 0)$, and $E^* = (x^*, y^*) = \left(\dfrac{c_1}{\beta}, \dfrac{r_1(K_1\beta - c_1)}{\alpha\beta K_1}\right)$. In order to have a positive equilibrium

point we assume that $K_1\beta - c_1 > 0$, that is, $0 < E < \dfrac{r(K\beta - c)}{(K\beta + r)}$. Under this assumption the

equilibrium point E^* occurs in the first quadrant. For $\tau = 0$, model (4) is reduced to model (2). Consequently, the equilibrium point E^* of model (4) is also globally asymptotically stable when $0 < E < \dfrac{r(K\beta - c)}{(K\beta + r)}$ whenever $\tau = 0$.

In order to understand the locally asymptotically stability of the equilibrium point E^* in the model with time delay, we analyze the associated linearization model with perturbation. Let $u(t) = x(t) - x^*$ and $v(t) = y(t) - y^*$. Then substitute into model (4) to get

$$\dot{u}(t) = r_1\left(u(t) + x^*\right)\left(1 - \frac{u(t) + x^*}{K_1}\right) - \alpha\left(u(t) + x^*\right)\left(v(t) + y^*\right)$$

$$\dot{v}(t) = -c_1\left(v(t) + y^*\right) + \beta\left(u(t-\tau) + x^*\right)\left(v(t-\tau) + y^*\right).$$

After simplifying and neglecting the product terms, we have the linearized model

$$\dot{u}(t) = \left(r_1 - \frac{2r_1}{K_1}x^* - \alpha y^*\right)u(t) - \alpha x^* v(t)$$

$$\dot{v}(t) = \beta y^* u(t-\tau) - c_1 v(t) + \beta x^* v(t-\tau).$$

Analyzing the local stability of the equilibrium point E^* in the model with time delay is equivalent to analyzing the stability of the zero equilibrium point in the linearized model. From the linearized model we have the characteristic equation

$$f(\lambda) = \begin{vmatrix} \lambda - \left(r_1 - \dfrac{2r_1}{K_1}x^* - \alpha y^*\right) & \alpha x^* \\ -\beta y^* e^{-\lambda\tau} & \lambda + c_1 - \beta x^* e^{-\lambda\tau} \end{vmatrix} = 0$$

$$\Delta(\lambda, \tau) = \lambda^2 - P\lambda e^{-\lambda\tau} + Q\lambda + Re^{-\lambda\tau} - S = 0,$$

(5)

where $P = \beta x^*$, $\qquad Q = c_1 - r_1 + \alpha y^* + \dfrac{2r_1 x^*}{K_1}$, $\qquad R = \beta r_1 x^* - \dfrac{2\beta r_1 (x^*)^2}{K_1}$, and

$S = \left(r_1 - \alpha y^*\right)c_1 - \dfrac{2r_1 c_1 x^*}{K_1}$. For $\tau = 0$ the characteristic equation becomes

$$\lambda^2 + (-P + Q)\lambda + R - S = 0 \tag{6}$$

which has the roots $\lambda_{1,2} = \dfrac{-(Q - P) \pm \sqrt{(Q - P)^2 - 4(R - S)}}{2}$. $\tag{7}$

We have $Q - P = \dfrac{r_1 c_1}{\beta K_1}$ and $R - S = \dfrac{c_1 r_1 (K_1 \beta - c_1)}{\beta K_1}$. Under the assumptions $r > E$ and

$K_1 \beta - c_1 > 0$, then $Q - P$ and $R - S$ are both positive numbers. Further, the eigenvalues of the characteristic equation (6) have negative real parts.

Theorem 1.

Let $\tau = 0$ and $0 < E < \dfrac{r(K\beta - c)}{(K\beta + r)}$. Then the equilibrium point E^* of model (4) is asymptotically stable.

Proof. From the condition $0 < E < \dfrac{r(K\beta - c)}{(K\beta + r)}$ we get the equilibrium point E^* in the positive quadrant. Since $\tau = 0$, then the eigenvalues of the characteristic equation (6) have negative real parts. Then we conclude that the equilibrium point E^* is asymptotically stable. $\square$

Now for $\tau \neq 0$, if $\lambda = i\omega$, $\omega > 0$, is a root of the characteristic equation (5), then we have

$$-\omega^2 - iP\omega\cos(\omega\tau) - P\omega\sin(\omega\tau) + Qi\omega + R\cos(\omega\tau) - Ri\sin(\omega\tau) - S = 0.$$

Separating the real and imaginary parts, we have

$$\begin{aligned} -\omega^2 - S - P\omega\sin(\omega\tau) + R\cos(\omega\tau) &= 0, \\ Q\omega - P\omega\cos(\omega\tau) - R\sin(\omega\tau) &= 0. \end{aligned} \tag{8}$$

Equivalently

$$\begin{aligned} \omega^2 + S &= -P\omega\sin(\omega\tau) + R\cos(\omega\tau), \\ Q\omega &= P\omega\cos(\omega\tau) + R\sin(\omega\tau). \end{aligned}$$

Squaring both sides gives

$$\omega^4 + 2S\omega^2 + S^2 = P^2\omega^2 \sin^2(\omega\tau) - 2PR\omega\sin(\omega\tau)\cos(\omega\tau) + R^2 \cos^2(\omega\tau)$$

$$Q^2\omega^2 = P^2\omega^2 \sin^2(\omega\tau) + 2PR\omega\sin(\omega\tau)\cos(\omega\tau) + R^2 \cos^2(\omega\tau).$$

Adding both equations and regrouping by powers of ω, we obtain the following fourth degree polynomial

$$\omega^4 - \left(P^2 - 2S - Q^2\right)\omega^2 + S^2 - R^2 = 0, \tag{9}$$

from which we obtain

$$\omega_\pm^2 = \frac{1}{2}\left\{\left(P^2 - 2S - Q^2\right) \pm \sqrt{\left(P^2 - 2S - Q^2\right)^2 - 4(S^2 - R^2)}\right\}. \tag{10}$$

From equation (10), it follows that if

$$Q^2 + 2S - P^2 > 0 \text{ and } S^2 - R^2 > 0, \tag{11}$$

then the equation (9) does not have any real solutions. To find the necessary and sufficient conditions for the nonexistence of time delay induced instability, we use the following theorem.

Theorem 2. (Kar, 2003)
A set of necessary and sufficient conditions for an equilibrium point $\left(x_*,\, y_*\right)$ *to be asymptotically stable for all* $\tau \geq 0$ *is*
1. The real parts of all the roots of $\Delta(\lambda,\, 0) = 0$ *are negative.*
2. For all real ω *and* $\tau \geq 0$, $\Delta(i\omega,\, \tau) \neq 0$, *where* $i = \sqrt{-1}$.

Theorem 3.
If condition (11) and Theorem 4.7 are satisfied, then the equilibrium point E^* *is locally asymptotically stable for all* $\tau \geq 0$.

Proof. From the assumptions $r > E$, $K_1\beta - c_1 > 0$, and also $\tau = 0$, we have that $Q - P$ and $R - S$ are both positive. Then the eigenvalues of the characteristic equation (5) have negative real parts. From condition (11) and Theorem 2, we conclude that the equilibrium point E^* is locally asymptotically stable for all $\tau \geq 0$. $\square$

Let us consider model (3) with parameters $r = 1.5$, $K = 100$, $\alpha = 0.2$, $c = 2.5$, $\beta = 0.1$, and $E = 0.3$. The equilibrium point of the model is $E^* = \left(28.00,\, 3.90\right)$. For $\tau = 0$, the Jacobian matrix of the model associated with the equilibrium point E^* has eigenvalues $-0.21000 \pm 1.46284\, i$. This means that the equilibrium point of the model without time delay is stable. We can verify that the conditions (11) are satisfied, that is, $Q^2 + 2S - P^2 = 0.17640$ and $S^2 - R^2 = 0.36691$. In this case there is no time delay that induces instability. Some trajectories of $\left(x(t),\, y(t)\right)$ with various time delays are given in Figures 1 and 2.
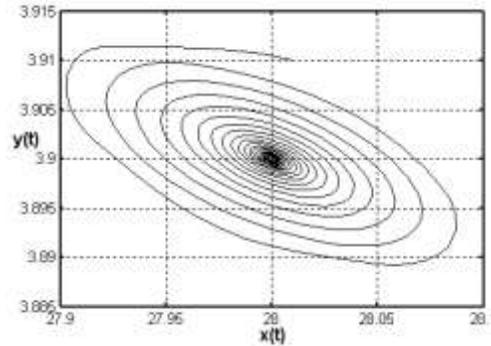
Figure 1. Trajectory of $(x(t), y(t))$ with $x(0) = 28.01$, $y(0) = 3.91$, and $\tau = 2.0$.
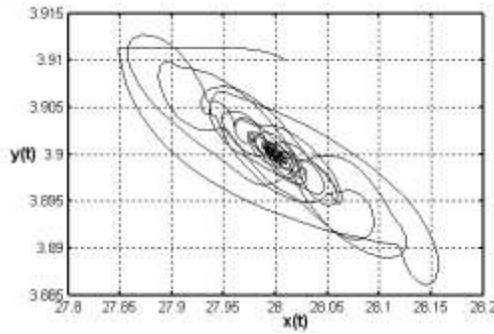
Figure 2. Trajectory of $(x(t), y(t))$ with $x(0) = 28.01$, $y(0) = 3.91$ and $\tau = 12.0$.

Figure 1 with time delay $\tau = 2.0$ shows that the trajectory of $(x(t), y(t))$ spirally tends to the equilibrium point. Figures 2 with time delay $\tau = 12.0$ shows that the equilibrium point $(28.00, 3.90)$ is still stable even if we increase the value of time delay. The trajectory of $(x(t), y(t))$ still tends to the equilibrium point as time goes on but there is no more a certain pattern of the behavior of the trajectory. From (10) we can verify that there is a unique positive solution of ω_0^2 if

$$S^2 - R^2 < 0. \tag{12}$$

We can now find the value of τ_k^0 by substituting ω_0^2 into equation (8) and solving for τ. We get

$$-\omega_0^2 - S - P\omega_0 \sin(\omega_0\tau) + R\cos(\omega_0\tau) = 0,$$
$$Q\omega_0 - P\omega_0 \cos(\omega_0\tau) - R\sin(\omega_0\tau) = 0.$$

Multiply the first equation with R and the second equation with $P\omega_0$ and subtract to get

$$-\left(R\omega_0^2 + RS + PQ\omega_0^2\right) + \left(R^2 + P^2\omega_0^2\right)\cos(\omega_0\tau) = 0.$$

Again, multiply the first equation with $P\omega_0$ and the second equation with R and add them to get

$$-\left(P\omega_0^3 + PS\omega_0\right) + QR\omega_0 - \left(R^2 + P^2\omega_0^2\right)\sin(\omega_0\tau) = 0.$$

Syamsuddin Toaha

Then we get

$$\tau_k^0 = \frac{\theta}{\omega_0} + \frac{2k\pi}{\omega_0}, \tag{13}$$

where $0 \le \theta < 2\pi$, and $\tan\theta = \dfrac{\omega_0(-P\omega_0^2 - PS + QR)}{(R\omega_0^2 + RS + PQ\omega_0^2)}$, with $k = 0, 1, 2, \cdots$.

Again, if

$$S^2 - R^2 > 0, \quad P^2 - 2S - Q^2 > 0, \text{ and}$$
$$\left(P^2 - 2S - Q^2\right)^2 > 4(S^2 - R^2) \tag{14}$$

hold, then there are two positive solutions of $\omega_\pm^2$. Substituting $\omega_\pm^2$ into equation (8) and solving for τ, we obtain

$$\tau_k^\pm = \frac{\theta_\pm}{\omega_\pm} + \frac{2k\pi}{\omega_\pm}, \tag{15}$$

where $0 \le \theta_\pm < 2\pi$, and $\tan\theta_\pm = \dfrac{\omega_\pm(-P\omega_\pm^2 - PS + QR)}{(R\omega_\pm^2 + RS + PQ\omega_\pm^2)}$, whit $k = 0, 1, 2, \cdots$.

Differentiating equation (5) with respect to τ, we obtain

$$\left(2\lambda + Q - Pe^{-\lambda\tau} - \tau(-P\lambda + R)e^{-\lambda\tau}\right)\frac{d\lambda}{d\tau} = \lambda\left(-P\lambda + R\right)e^{-\lambda\tau}$$

therefore

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{2\lambda + Q}{\lambda\left(-P\lambda + R\right)e^{-\lambda\tau}} + \frac{-P}{\lambda\left(-P\lambda + R\right)} - \frac{\tau}{\lambda}$$

From equation (5), we have $e^{-\lambda\tau} = \dfrac{-\left(\lambda^2 + Q\lambda - S\right)}{\left(-P\lambda + R\right)}$, then we obtain

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{2\lambda + Q}{-\lambda\left(\lambda^2 + Q\lambda - S\right)} + \frac{-P}{\lambda\left(-P\lambda + R\right)} - \frac{\tau}{\lambda}$$

Thus,

$$\text{sign}\left\{\frac{d(\text{Re }\lambda)}{d\tau}\right\}_{\lambda=i\omega} = \text{sign}\left\{\text{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}\right\}_{\lambda=i\omega}$$

$$= \text{sign}\left\{\text{Re}\left(\frac{2\lambda + Q}{-\lambda\left(\lambda^2 + Q\lambda - S\right)}\right)_{\lambda=i\omega} + \text{Re}\left(\frac{-P}{\lambda(-P\lambda + R)}\right)_{\lambda=i\omega} + \text{Re}\left(\frac{-\tau}{\lambda}\right)_{\lambda=i\omega}\right\}$$

$$= \text{sign}\left\{\text{Re}\left(\frac{2i\omega + Q}{-i\omega\left(-\omega^2 + Qi\omega - S\right)}\right) + \text{Re}\left(\frac{-P}{i\omega(-Pi\omega + R)}\right) + \text{Re}\left(\frac{-\tau}{i\omega}\right)\right\}$$

$$= \text{sign} \left\{ \frac{Q^2 + 2\omega^2 + 2S}{Q^2\omega^2 + \left(\omega^2 + S\right)^2} - \frac{P^2}{\left(P^2\omega^2 + R^2\right)} \right\}.$$

From equation (9), we know that

$$P^2\omega^2 + R^2 = \omega^4 + \left(Q^2 + 2S\right)\omega^2 + S^2 = Q^2\omega^2 + \left(\omega^2 + S\right)^2$$

then we obtain

$$\text{sign} \left\{ \frac{d(\text{Re}\,\lambda)}{d\tau} \right\}_{\lambda=i\omega} = \text{sign} \left\{ \frac{Q^2 + 2\omega^2 + 2S}{Q^2\omega^2 + \left(\omega^2 + S\right)^2} - \frac{P^2}{Q^2\omega^2 + \left(\omega^2 + S\right)^2} \right\}$$

$$= \text{sign} \left\{ 2\omega^2 - \left(P^2 - 2S - Q^2\right) \right\}. \tag{16}$$

Theorem 4.

If condition (12) is satisfied, then the equilibrium point E^* is asymptotically stable for $\tau < \tau_0$ and unstable for $\tau > \tau_0$. Further, as τ increases through τ_0, the equilibrium point E^* bifurcates into small amplitude periodic solutions, where $\tau_0 = \tau_k^0$ as $k = 0$.

Proof. For $\tau = 0$ and under the assumptions $r > E$ and $K_1\beta - c_1 > 0$, then $Q - P$ and $R - S$ are both positive. It means that the equilibrium point E^* is asymptotically stable. Hence, following the proof of Theorem in Kuang, 1993, page 66, the equilibrium point E^* remains stable for $\tau < \tau_0$. We now have to show that $\left.\dfrac{d(\text{Re}\,\lambda)}{d\tau}\right|_{\tau=\tau_0,\,\omega=\omega_0} > 0$. This will signify that there

exists at least one eigenvalue with positive real part for $\tau > \tau_0$. Moreover, the conditions of Hopf bifurcation are then satisfied yielding the required periodic solution, see Hale (1977), Broer (1983), and Nayfeh and Balachandran (1995). From (16) and (10), it follows that

$$\text{sign} \left\{ \frac{d(\text{Re}\,\lambda)}{d\tau} \right\}_{\lambda=i\omega_0} = \text{sign} \left\{ 2\omega_0^2 - \left(P^2 - 2S - Q^2\right) \right\}$$

$$= \text{sign} \left\{ \sqrt{\left(P^2 - 2S - Q^2\right)^2 - 4\left(S^2 - R^2\right)} \right\},$$

then we get

$$\left. \frac{d(\text{Re}\,\lambda)}{d\tau} \right|_{\tau=\tau_0,\,\omega=\omega_0} > 0 \ .$$

Therefore, the transversality condition is satisfied, and hence, the Hopf bifurcation occurs at $\omega = \omega_0$, $\tau = \tau_0$. This completes the proof. $\square$

Now we consider again model (3) with parameters $r = 1.5$, $K = 100$, $\alpha = 0.2$, $c = 2.0$, $\beta = 0.1$, and $E = 0.3$. The equilibrium point of the model is $E^* = (23.00, 4.275)$. For $\tau = 0$, the Jacobian matrix of the model associated with the equilibrium point E^* has

eigenvalues $-0.17250\pm1.39167\,i$. This means that the equilibrium point of the model without time delay is stable. It is easy to verify that the condition (12) is satisfied, that is, $S^2 - R^2 = -0.74629 < 0$. Further, we have $\omega_0 = 0.89800$ and $\tau_0 = 0.56911$. Some trajectories of $(x(t),\ y(t))$ with various time delays are given in Figures 3, 4, and 5.
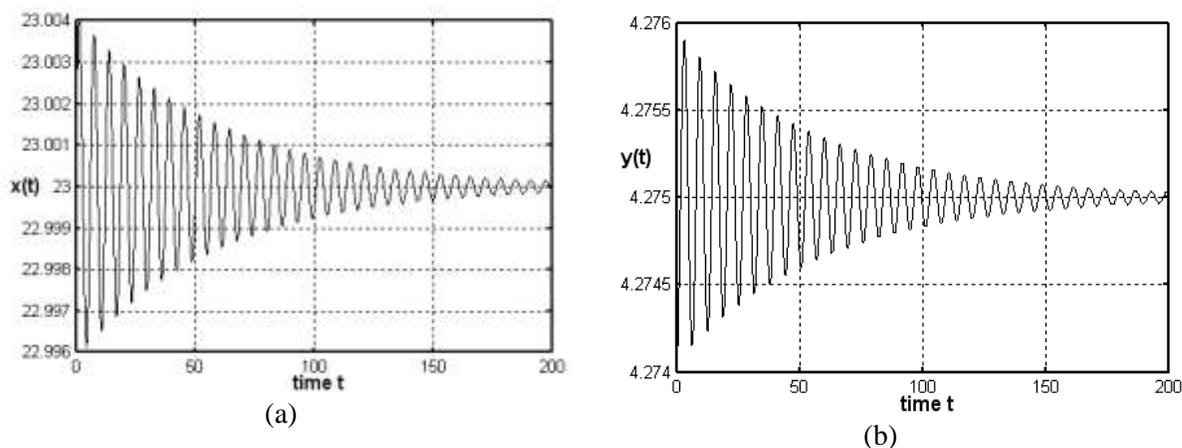
Figure 3. (a) Trajectory of Prey with $x(0) = 23.001$ and $\tau = 0.4$; (b) Trajectory of Predator with $y(0) = 4.274$ and $\tau = 0.4$.
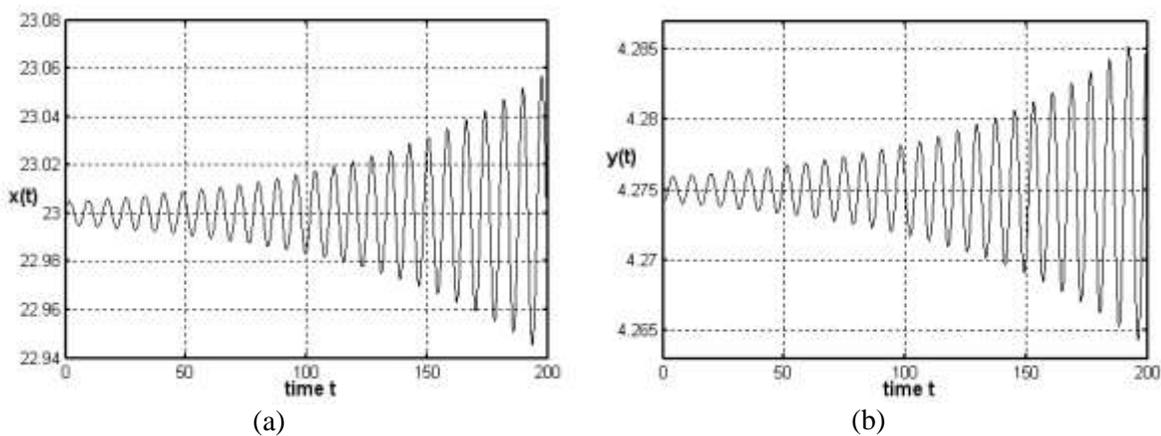
Figure 4. (a) Trajectory of Prey with $x(0) = 23.001$ and $\tau = 0.8$; (b) Trajectory of Predator with $y(0) = 4.274$ and $\tau = 0.8$.
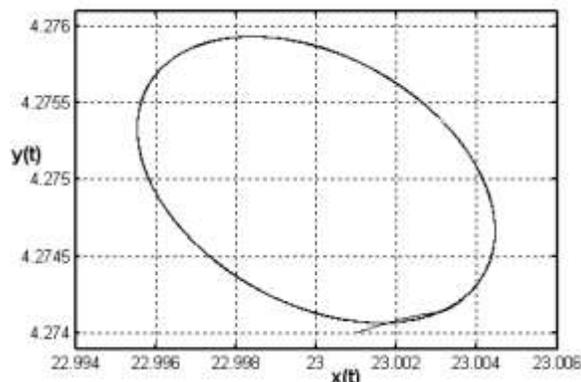
Figure 5. Trajectory of $(x(t),\, y(t))$ with $x(0) = 23.001,\ y(0) = 4.274$,
and $\tau = 0.56911$.

Figures 3a and 3b with time delay $\tau = 0.4$ show that the equilibrium point $(23.00,\, 4.275)$ is stable. Figures 4a and 4b with time delay $\tau = 0.8$ show that the equilibrium point $(23.00,\, 4.275)$ is unstable. The critical value of time delay or delay margin is $\tau_0 = 0.56911$. When $0 \leq \tau < 0.56911$ the equilibrium point $(23.00,\, 4.275)$ is asymptotically stable; when $\tau = 0.56911$ the equilibrium point $(23.00,\, 4.275)$ loses its stability; and when $\tau > 0.56911$ the equilibrium point $(23.00,\, 4.275)$ becomes unstable and there is a bifurcating periodic solution, see figure 5.

Theorem 5.

Let $\tau_k^{\pm}$ be defined in equation (15). If conditions (14) are satisfied, then there exists a positive integer m such that there are m switches from stability to instability and to stability. In other words, when $\tau \in [0,\, \tau_0^+) \bigcup (\tau_0^-,\, \tau_1^+) \bigcup \cdots \bigcup (\tau_{m-1}^-,\, \tau_m^+)$, the equilibrium point E_1 is stable, and when $\tau \in (\tau_0^+,\, \tau_0^-) \bigcup (\tau_1^+,\, \tau_1^-) \bigcup \cdots \bigcup (\tau_{m-1}^+,\, \tau_{m-1}^-)$, the equilibrium point E^* is unstable. Therefore there are bifurcations at the equilibrium point E^* when $\tau = \tau_k^{\pm},\ k = 0, 1, 2, \cdots$.

Proof. Since conditions (14) are satisfied, then to prove the theorem we need only to verify the transversality conditions, see Cushing (1977),

$$\left.\frac{d(\operatorname{Re}\lambda)}{d\tau}\right|_{\tau=\tau_k^+} > 0 \quad \text{and} \quad \left.\frac{d(\operatorname{Re}\lambda)}{d\tau}\right|_{\tau=\tau_k^-} < 0.$$

From (16) and (10), it follows that

$$\operatorname{sign}\left\{\frac{d(\operatorname{Re}\lambda)}{d\tau}\right\}_{\lambda=i\omega_+} = \operatorname{sign}\left\{2\omega_+^2 - \left(P^2 - 2S - Q^2\right)\right\} = \operatorname{sign}\left\{\sqrt{\left(P^2 - 2S - Q^2\right)^2 - 4\left(S^2 - R^2\right)}\right\},$$

therefore,

$$\left.\frac{d(\operatorname{Re}\lambda)}{d\tau}\right|_{\omega=\omega_+,\,\tau=\tau_k^+} > 0.$$

Again,

$$\text{sign}\left\{\frac{d(\text{Re }\lambda)}{d\tau}\right\}_{\lambda=i\omega_-} = \text{sign}\left\{2\omega_-^2 - \left(P^2 - 2S - Q^2\right)\right\} = \text{sign}\left\{-\sqrt{\left(P^2 - 2S - Q^2\right)^2 - 4\left(S^2 - R^2\right)}\right\},$$

therefore,

$$\left.\frac{d(\text{Re }\lambda)}{d\tau}\right|_{\omega=\omega_-,\tau=\tau_k^-} < 0.$$

Hence, the transversality conditions are satisfied. This completes the proof. □

After simplifying we know that $P = c_1$, $Q = \dfrac{c_1(\beta K_1 + r_1)}{\beta K_1}$, and $S = -\dfrac{r_1 c_1^2}{\beta K_1}$ from which we have $P < Q$. Further we have $P^2 - Q^2 < 0$ and then $P^2 - 2S - Q^2 < 0$. Consequently, it is impossible to have two positive solutions of $\omega_\pm^2$ and we verify that there is no any switch from stability to instability and to stability for model (3).

4. Conclusions

The model without time delay has one positive equilibrium point and stable. The same equilibrium point is found for the model with time delay. The stability of the positive equilibrium point for the model with time delay is free from the effect of time delay when condition (11) is satisfied.

When condition (12) hold, there exists a delay margin for which a Hopf bifurcation occur and when the value of time delay is greater than the delay margin, then the equilibrium point becomes unstable. While when condition (14) is satisfied, the time delay can induce instability and some Hopf bifurcations occur. We found finite stability intervals for the equilibrium point.

For the model with time delay and constant effort of harvesting, there still exists a positive equilibrium point. The positive equilibrium point may or may not be stable. It is depend on the values of effort of harvesting and time delay. The time delay can affect the stability of the equilibrium point. There exist some conditions for the effort and time delay that assure the stability of the positive equilibrium point.

References

[1]   Berryman, A.A., 1992, The origins and evolution of the predator-prey theory, *Ecology,* 73:1530-1535.

[2]   Broer, H.W., 1983, Quasi periodicity in local bifurcation theory, *In Bifurcation, Theory, Mechanics and Physics*, ed. C.P. Bruter, A. Aragnol and A. Lichnerowicz, pp 177-208. Dordrecht: D. Reidel Publishing Company.

[3]   Cushing, J.M., 1977, *Integrodifferential equations and delay models in population dynamics*. Heidelberg: Springer-Verlag.

Syamsuddin Toaha

[4] Gourley, S.A. and Kuang, Y., 2004, A stage structured predator-prey model and its dependence on maturation delay and death rate, *J. Math. Biol*, 49:188-200.

[5] Hale, J.K., 1977, *Theory of functional differential equations*. Heidelberg: Springer-Verlag.

[6] Kar, T.K., 2003, Selective harvesting in a prey-predator fishery with time delay, *Mathematical and Computer Modelling,* 38:449-458.

[7] Kuang, Y., 1993, *Delay differential equations with application in population dynamics*, New York: Academic Press.

[8] Kuang, Y. and Beretta, E., 1998, Global qualitative analysis of a ratio-dependent predator-prey system, *J. Math. Biol*., 36:389-406.

[9] Li, Y. and Kuang, Y., 2001, Periodic solutions in periodic delayed Gause-type predator-prey systems, *Proceedings of Dynamical Systems and Applications,* 3:375-382.

[10] Liu, Z. and Wang, W., 2004, Persistence and periodic solution of a nonautonomous predator-prey diffusion system with Holling III functional response and continuous delay, *Discrete and Continuous Dynamical System,* Series B 4(3):653-662.

[11] Martin, A. and Ruan, S., 2001, Predator-prey models with delay and prey harvesting, *Journal of Math. Biol*., 43:247-267.

[12] Nayfeh, A.H. and Balachandran, B., 1995, *Applied nonlinear dynamics*, New York: John Wiley & Sons.

[13] L. Qiu, and Mitsui, T., 2002, Predator-prey dynamics with delay when prey dispersing in n-paths environment, Online Journal, http://www.math.human. nagoyau.ac.jp/preprint/ 2002-1.pdf [Accessed on 20 July 2004]

[14] Toaha, S., Hassan, M.A., Ismail, F. and June, L.W., 2007, Stability analysis of prey-predator population model with harvesting, submitted to *J. IRSIAM*